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Primary Production of Phytoplankton in the Three Types of Amazonian Waters
V. Some Investigations on the Phytoplankton and its Primary Productivity in the Clear Water of the Lower Rio Tapajóz (Pará, Brazil)*

by

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1. Introduction

Besides white and blackwaters in Amazonian rivers and lakes, a third type can be defined – clearwater – which is characterized by its low concentrations of sediments and dissolved electrolytes, as well as by small amounts of humic substances (SIOLI 1950, 1964, 1965, 1968). The relative distribution of ions is comparable to patterns known from other fresh water types in the world, only their absolute concentration is much lower. Earth alcaline carbonates are dominating, thus providing the base for well-balanced chemical conditions as in regard to pH (SCHMIDT 1972).

The lower Rio Tapajóz was chosen as a typical clearwater river for investigations on primary production of phytoplankton in the three Amazonian water types, which were conducted from 1967 - 1970 (SCHMIDT 1973a).

Although the results were not published before now, their significance can still be considered as of immediate interest. As already mentioned before (SCHMIDT 1973a), we should like to thank all those who made our work possible.

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* Herrn Prof. Dr. H. Sioli, Plön, zum 70. Geburtstag gewidmet.

2. Sampling conditions

Between june 1968 and december 1969 a total of four excursions to the Rio Tapajóz were conducted. Sampling sites (Fig. 1) and their specific conditions are presented below.

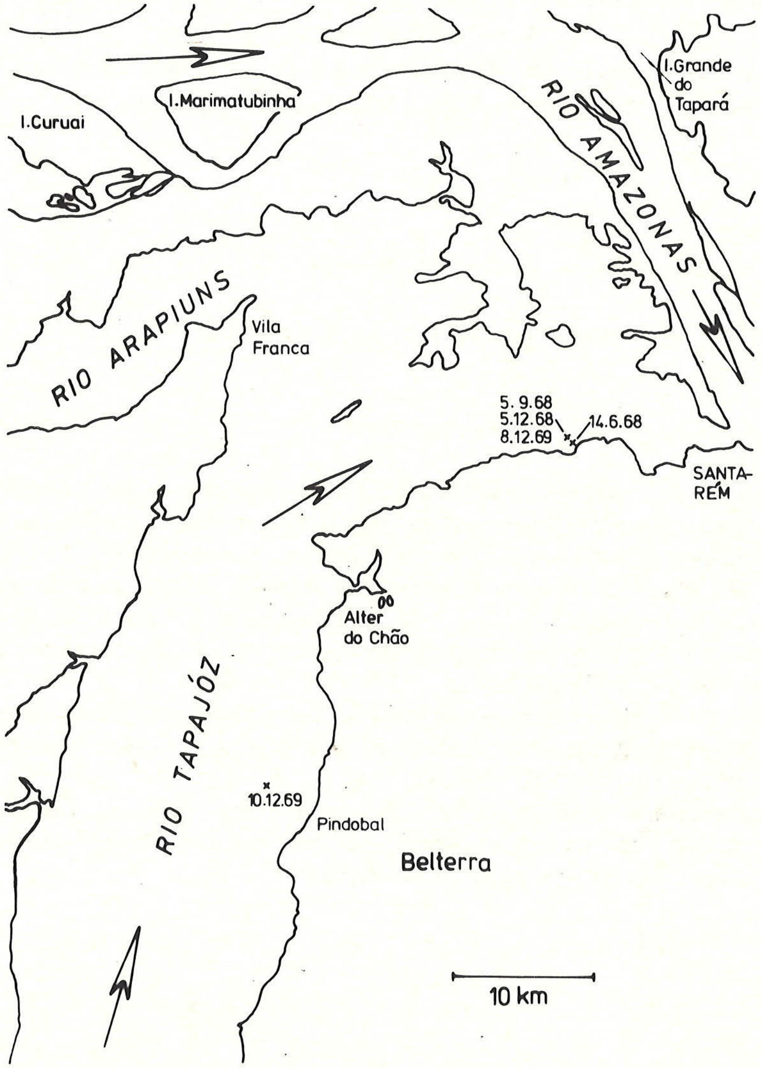

Fig. 1:
Map showing the position of the sampling sites

Table 1: Sampling sites and -conditions

date	position	distance off shore	waterdepth	waterlevel
14.-15. 6.68	ca. 15 km above Santarém	ca. 500 m	ca. 10 m	close to maximum, slightly falling
5.- 6. 9.68	ca. 15 km above Santarém	ca. 1000 m	ca. 14 m	two meters below june level, still falling
5.- 6.12.68	ca. 15 km above Santarém	ca. 1000 m	ca. 12 m	still slightly falling, almost lowest level
8.- 9.12.69	ca. 15 km above Santarém	ca. 1000 m	ca. 10 m	minimum level, stagnant
10.-11.12.69	ca. 50 km above Santarém, slightly above Pindobal	ca. 3000 m	ca. 8 m	same as 8.12.69

3. Methods

The methods for the determination of physical-chemical parameters were the same as described earlier (SCHMIDT 1973b). Conductivity, pH, free carbonic acid, and total carbon were determined in situ, while the other analysis were run at the limnological laboratories of INPA, Manaus.

Data for primary production of phytoplankton were gathered by applying the C-14 method. Samples were taken at around 7 a.m., and the exposition of light and dark bottles lasted 24 hours, beginning at 8 a.m. More detailed informations have been presented and discussed earlier (SCHMIDT 1973c). Chlorophyll-a determination of seston samples after extraction in ethanol, was derived from comparison with a Chlorophyll-a calibration curve (SCHMIDT 1973c). Plankton concentration data were derived from net catches (Höll-Netz, 10 microns diameter), and membrane-filter samples served for counting the number of organisms.

4. Results

4.1. Physical-chemical conditions

The results of these investigations are comprised in tables 2 and 3.

Table 2: General physico-chemical properties of the water and carbon contents of the Rio Tapajóz (0 m)

						Rio Amazonas
Date	14.6.68	5.9.68	6.12.68	8.12.69	10.12.69	15.12.69
water temperature/°C	28,7	29,4	28,8	29,3	29,0	29,8
electr. conductivity µS 20/cm	11,9	14,0	15,2	14,7	13,5	67,8
pH	6,5	6,6	6,7	7,2	6,6	7,3
alcalinity (SBV) mval/l	0,12	0,12	0,14	0,16	0,14	0,51
HCO_3^- ppm	7,32	7,32	8,54	9,76	8,54	31,11
fix. CO_2 ppm	5,3	5,3	6,2	7,0	6,2	
free CO_2 ppm	2,9	8,6	1,5	1,0	1,5	
total-C (inorgan.) ppm	2,2	3,8	2,1	2,2	2,0	
Secchi-transparency m	3,2	3,9	3,1	2,6	2,0	
color of the water ppm Pt/l				9,8	12,1	25,7

Table 3: Plant nutrients of the Rio Tapajóz (0 m)

						Rio Solimões	Rio Amazonas
Date	14.6.68	5.9.68	6.12.68	8.12.69	10.12.69	23.12.69	15.12.69
total Hardness °dH	0,12	0,22	0,24	0,25	0,25	1,7	1,3
Ca^{++} ppm	0,8	1,03	1,53	1,25	1,25	9,2	7,2
Mg^{++} ppm	0,3	0,35	0,70	0,32	0,32	1,7	1,2
Fe dissolv. ppb	80	25	30	50	60	790	590
Fe susp. ppb	55	60	70	40	40	3310	1310
Fe total ppb	135	85	100	90	100	4100	1900
N (NO_2^-) ppb	2	< 1	< 1	2	2	4	2
N (NO_3^-) ppb	8	< 1	2	3	3	71	4
Kjeldahl-N ppb	248	240	336	430	400	670	570
Total-N ppb	258	240	338	435	405	745	576
P (PO_4^{3-}) ppb				< 1	< 1	15	15
Total-P ppb	8	11	12	21	15	136	66
Cl^- ppb	1,9	1,7	1,5	1,6	1,6	3,1	4,1
Si ppb				2,1	2,8	3,6	3,7

No significant differences could be found when comparing the results from different water depths, which indicates that stratification did not occur in the Rio Tapajóz during the investigation period. Although the water flow is low (on its last 110 km before its confluent with the Amazon river, the Rio Tapajóz is about 14 km wide), stratification of the water body evidently seem to be rare. Probably this is due to the low water depth and quite constant winds blowing from the northeast, which also during the night hours diminish only

slightly. Consequentely the data in tables 2 and 3 present only values from 0 m water depth. For comparison, additional results from the Amazon river are given, which were collected from above the confluent with the Rio Tapajóz.

Although no stratification was found at the main sampling sites, additional studies showed that in protected water bodies, close to the banks, considerable vertical differences in temperature, pH, and phytoplankton distribution occasionally occur (Fig. 2).

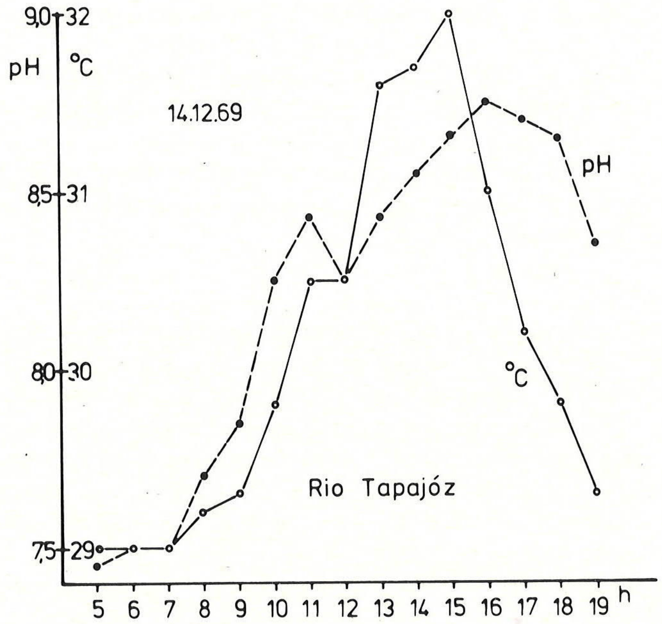

Fig. 2:
Diurnal variations of the water temperature and pH in a bay of the lower Rio Tapajóz at 14/12/69 (Station = about 40 km upstream of Santarém; about 50 m off of the right bank)

Table 3 gives a description of common plant nutrients. It is obvious that carbonates, and especially Ca^{++}-carbonate, represent the determining factors for salinity. Nitrates, nitrites and phosphates could be detected only in minute concentrations, close to the limits of detectability. Considerably higher are the values for Kjeldahl-N, which mainly consists of plankton-fixed nitrogen. Noteworthy are further on the iron concentrations, suggesting

that this element is always abundant in sufficient quantities for phytoplankton. Similar contents of dissolved iron have recently been described by GEISLER and SCHNEIDER (1976).

While, as mentioned above, vertical stratifications can hardly be expected in the open river, fluctuations with the hours of a day of pH and temperature, seem to be more distinct, especially in protected bodies along the banks. On the 12.12.68 the pH of the Rio Tapajóz, measured close to the shore, was 7.37 at 7.30 a.m., then reached its peak of 8.85 at 1.30 p. m. followed by a decrease.

Another good example for such fluctuations in a small river bay offshore is listed in fig. 2. The highest pH value was 8.75 (electric method). A phenolphthalein control gave a clear change in colour. During the december excursion in 1969, pH values of more than 8.4 were detected several times, also at considerable distance from the bank. Unfortunately, lack of time prevented further investigations of this phenomenon, especially its relation to space and time.

Of course, the considerable alterations in the course of pH during a day undoubtedly are the result of photosynthetic plankton activities. This clearly indicates that during certain periods of the day, CO_2 availability can become a limiting factor for algae production. This is not surprising, since due to the low total concentration of dissolved calcium, biogenic decalcification is only possible within a very narrow range. Comparable situations are also known to occure in várzea lakes (SCHMIDT 1973b).

4.2. Qualitative and quantitative aspects of phytoplanktonic distribution

In 1976 UHERKOVICH published detailed results of his qualitative investigations of the 1968-material. Only the samples which were collected in 1969 have not yet been evaluated. With regard to the taxonomic composition of phytoplankton we refer to the above mentioned. Some of the most relevant aspects of his results are: Different from other Amazonian waters, species variety is extremely high in the Rio Tapajóz. Especially manyfold are the desmidiaceae (see also GRÖNBLAD 1945, THOMASSON 1971 and FÖRSTER 1969).

Their total number, however, is very low in the majority of the samples. The dominating groups consist of mostly a few species of cyanophyceae, diatomeae and some chlorophyceae. UHERKOVICH describes the order of precedence regarding the relative abundance of the following taxa:

Cyanophycea	*Anabaena hassalii*
	Anabaena spiroides
	Oscillatoria limosa
	Microcystis aeruginosa
Diatomea	*Melosira granulata*
	Melosira granulata var. *angustissima*
	Rhizosolenia longiseta
	Synedra acus
Chlorophyta	*Treubaria crassispina*
	Pediastrum duplex
Conjugatae	*Mougeotia* spec.

Some extremely small forms, probably cyanophyceae of the coccal type, were hard to identify and could thus not be included. Still remains to be mentioned that because of their large numbers, it cannot be denied that some importance in the whole system might be attributed to them.

Table 4: Counting results (numbers of cells/ml) of the most importent members of phytoplankton (means of the results for the different water depths)

Date	14.6.68	5.9.68	6.12.68	8.12.69	10.12.69
investigated water depths	0 - 7 m	0 - 14 m	0 - 14 m	0 - 7 m	0 - 7 m
numbers of samples (n)	4	8	7	6	6
Anabaena	6	304	75	622	2458
Oscillatoria	336	143	105	317	439
Microcystis	201	122	255	1202	358
Melosira	99	84	821	609	583
other Diatomeae	94	104	62	41	20
Chlorophyta (except Desmidiac.)	1098	344	457	737	2816
Desmidiaceae	8	21	83	52	84

Table 4 informs about the concentrations of the most frequently encountered organisms from membrane filter samples. At least those samples which were collected in the morning time show no clear tendencies towards vertical stratifications, as this shown was above for the chemical factors. For this reason only the calculated average numbers of cells/ml from different depths are given. The same applies to filamentous and group-forming organisms such as oscillatoria or microcystis, which some authors describe according to the number of filaments or aggregates.

Since aggregates often fall in pieces during the preparation process, the definition of cells per ml was chosen as the most propriate and logical one for presentation. The relevance of the most important forms and types in terms of production and abundance is emphasized by tabulating the results of a few compromised groups only. It is clear that cell size variations amongst species must be considered for the exact evaluation of biomass-proportions.

In Table 4 some genera were seperated according to their significance, while others are comprised into larger units, since no striking differences in quantities between either genera or species could be generally noticed.

Despite of their low abundance the strongly differenciated desmidiaceae were seperated from chlorophyta in order to point out their relatively unimportant quantitative significance.

Summarising the results of Table 4, it can be stated that relatively few organisms are of importance for the total biomass production throughout the year. Variations among certain species, as e. g. anabaena and melosira, could be observed. The latter was extremely numerous during the low water period.

As could be shown in earlier investigations (SCHMIDT and UHERKOVICH 1973), specific ecological interactions in the Rio Tapajóz cannot be characterized by an isolated consideration of numerically dominating plankton organisms. Though they are cosmopolitans of immense ecological valence, the characteristic features of the Rio Tapajóz phytoplankton structure, and consequently also specific ecological and bio-geographic conditions, can only be understood when also considering the importance of many, numerically less important taxa of which extensive lists have been published (GRÖNBLAD 1945, SCOTT et al. 1965, FÖRSTER 1969, THOMASSON 1971, UHERKOVICH 1976). Maybe because of their morphological peculiarities, the desmidiaceae receive more attention than others.

Our present knowledge of causal relationships regarding the enormous taxonomic diversity is still quite incomplete.

4.3. Primary Production of Phytoplankton

Primary production data are listed in fig. 3 and table 5.

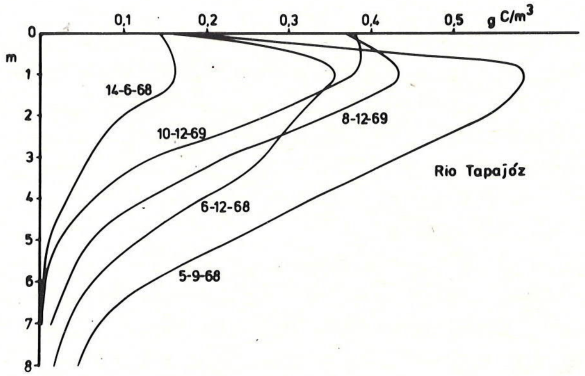

Fig. 3:
Vertical pattern of net primary productivity of phytoplankton during the 24 hour exposure at the different sampling days

Table 5: Production and C-turn-over rates

Date	Chlorophyll-a mg/m^2	algae-C g/m^2	net prod. $gC/m^2/d$	gross. prod. $gC/m^2/d$	C-turnover time in days
14. 6.68	81	1,22	0,442	0,56	2,2
5. 9.68	61	0,92	2,413	2,74	0,3
6.12.68	149	2,24	1,444	1,74	1,3
8.12.69	89	1,34	1,432	1,74	0,8
10.12.69	162	2,43	1,099	1,41	1,7
			ø 1,366		

The thickness of the trophic layer varies between 5 and 10 meters. A clear relationship exists between thickness and transparency (Secchi-disk), and the thickness of the production zone is about twice that of Secchi transparency or even more. This confirms the lack of other seston, except for the phytoplankton itself.

The fact that production curves in fig. 3 have their peaks clearly beneath and not at the surface, again proves the existence of exellent light conditions.

Larger deviations for total production can be observed in june and september 1968, while the three surveys undertaken during the low water period show better corresponding data. Both production density (Fig. 3) and production per unit area (Table 5) are highest in september 1968. At the same time transparency reaches its maximum, but absolute plankton concentration is lowest, as algae-C- and chlorophyll concentration indicate (Table 5).

The only explanation for this contradictory finding is an extremely short turn over time, which for the carbon turn over was found to be as short as 0.3 days only. The causative factors of this phenomenon are not yet known, and neither temperature nor the other physical and chemical parameters give satisfying clues for an interpretation of this rather complex situation, which was determined from various independent analysis.

An exact interpretation of all production parameters becomes possible only when keeping in mind the general problem of accuracy and applicability of methods. For example, OHLE showed in 1962 that the C-14 method principally produces only minimum results. The basic disadvantage of light- and dark flask experiments is increasing inaccuracy with prolonged time of exposition. Intervalls of less than 24 hours produce even more pronounced problems, however (SCHMIDT 1973c).

Under the given production conditions in the Rio Tapajóz (high temperature, good light conditions, small nutrition- and fair plankton concentration, but constant exchange processes between the eutrophic zone and deeper layers) it can be suggested that the actual production probably exceeds the experimentally one found, always provided that no other limiting factors occur.

One of such factors might be restricted carbon availability for assimilation purposes under certain conditions. The rise in pH underlines such an assumption. Evidently these

processes indicate that under specific conditions the turn over – especially for carbon assimilation – is faster than the vertical nutrient transport from deeper water leayers into the euphotic zone. On the other hand it might be that due to exchange processes, the reduction of certain elements occurs both in the euphotic zone and deeper layers. The fact that in the lower reaches of the Rio Tapajóz the euphotic zone probably amounts to considerably more than 50 % of the total water depth, supports the likelyhood of the latter assumption.

The average net production per unit area of all stations is 1.37 g $C/m^2/d$. Assuming a vegetation period of 365 days per year, net production of phytoplankton in the lower Rio Tapajóz could reach an estimated 500.05 g C/m^2, or ca 5 metric tons of carbon per hectare in one year. This production would be considerably higher than the one encountered in a Várzea-lake (Lago do Castanho) with 3.9 t C per year (SCHMIDT 1973c), where nutrient concentrations were higher but light conditions poor.

5. Discussion

The general characterization of the amazonian watertype "clearwater" as an expression of its physical and chemical properties, which was first recognized and defined by SIOLI (1950, 1965, etc.), becomes strong support from the results of our own investigations. The same is true for BRAUN's remarks (1952) on the Rio Tapajóz.

Under some aspects new findings or diverging facts could be documented. For example, neither BRAUN nor SIOLI mentioned such strong rises in pH covering areas as large as the ones we found in 1969.

The high densities of Melosira granulata and Anabena as described by BRAUN, could be confirmed in 1968 and 1969. Their large biomasses are still the majoring factor for autochthone primary production in the lower Rio Tapajóz. Also, temporary mass productions of these two forms, which can change the water color or even appear as algae blooms, were mentioned by BRAUN and could be observed again in december 1969 at Pindobal.

Some diverging results were found in regard to cell concentrations. The concentrations we found in one ml are of the same dimension as those given by BRAUN for one liter. Considering the fact that he mentioned the occurrence of algae blooms, and visibility was 2 m, as it was also in december 1969, one should expect to find identical concentrations in the samples. We believe that the diverging results probably were caused by calculation errors or by giving results as aggregates resp. filaments per unit volume and not as cells.

In comparison with the other amazonian water types, clear water shows the highest phytoplankton production rates of all. This seems to be surprising at first sight, but can easily be explained.

Although nutrient concentrations are lower than in white water or in decanted white water, extremely favourable light conditions throughout the year make such production rates possible. The trophic zone can penetrate into deeper water layers, which increases the production per unit area. Production density in decanted white water can temporarily be much higher, but the thickness of the euphotic layer is considerably less (SCHMIDT 1973c).

In black water, both light conditions and nutrient concentrations are disfavourable for primary production. In spite of seasonal variations which are possible to occur here, the average production level remains low (SCHMIDT 1976). The different requirements for primary production for the most important amazonian water types were formulated by FITTKAU et al. (1975), and are still applyable. For this reason we present his scheme below with only minor modifications (Table 6).

Litoral vegetation in black and clearwater is generally lacking, thus primary production depends almost exclusively on phytoplankton. In white water, even when decanted or mixed with different water types, the basis for autochthone primary production receives considerable support from organic substances produced by the floating meadows along the shores, and under the specific conditions of very small water systems, litoral production can substancially exceed phytoplankton production (SIOLI 1968, JUNK 1970).

The estimated conversion factor for algae-C into fish biomass (wet weight) is approximately 0.02 (SCHMIDT 1973c). This means that roughly 100 kg of organic carbon in form of algae would be neccessary for the production of 2 kg fish biomass. Based on a 5 t net production of carbon per hectare and year, a theoretical fish production of 100 kg can be expected. Although this calculated value would include different species and age groups which do not serve for direct human concumption, the result is surprisingly high. It must be questioned whether such fish production based on primary production can ever be reached.

Primary production in the Rio Tapajóz basicly depends on fast turn over rates of the most important elements, as this was pointed out before and can be proved by the results in table 5. Probably a system of short-circuit mechanisms interacts mainly between algae and bacteria. However, should the production-pyramid in the Rio Tapajóz comprise various levels of synchronized dependencies, including fish or other ultimate consumers, the main portion of biomass from the higher levels would have to be fed back and made available for primary production again. This appears to be a must, since nutrient input from upriver and other tributaries is low in comparison with the biomass of primary producers in the lower Rio Tapajóz.

Consequently a constant withdrawl of large amounts of fish would gradually reduce the total production

Of course, these questions concerning stock management cannot be satisfactorily discussed since too many factors involved in production patterns are still unknown. We suppose that under the given production situation a justifiable yearly amount of 10 to 20 kg of fish per hectare could be taken from the system without causing ecological problems. Theoretically a total of 1.500 to 3.000 tons of fish could be produced in the lower Rio Tapajóz every year and thus be made available for human consumption.

Bearing in mind the problems descussed by JUNK and HONDA (1976) and JUNK (1979), it is obvious, that further investigations are neccessary to increase our present knowledge on this topic.

Table 6: Requirements for primary production of phytoplankton in the three types of amazonian waters (acc. to FITTKAU et al. 1975)

Water	Example	Light conditions	Nutritional status	Phytoplankton density	Production per unit area	References
White water	Rio Solimões	bad	good	very low	very low	SCHMIDT 1973b, c
Decanted white and mixed water	Lago do Castanho	bad to moderately good	relatively good	high to very high	high	SCHMIDT 1973
Black water	Rio Negro	bad	very poor	very low	very low	SCHMIDT 1976
Clear water	Rio Tapajóz	good	poor	moderate	high	

6. Summary

Four limnological investigations were conducted in different seasons of the years 1968 and 1969 at the lower reaches of the Rio Tapajóz.

The physical and chemical parameters generally correspond with earlier findings of other authors.

Midriver areas show no stratification of the water body. In certain reaches of the river, distinct increases of pH-values temporarily occur due to strong phytoplankton activity.

A few species of cyanophyceae and diatomeae make up the vast majority of phytoplankton in terms of numbers. Chlorophyceae, desmidiaceae, and other algae are characterized by high species variety but only occur in low or moderate densities. Despite of the low nutrient concentrations encountered, phytoplankton production is high, which can be attributed to the excellent light conditions in the river. The net production of 2.4 g $C/m^2/d$ exceeds by far production rates from várzea-lakes, although production densities are lower. A mighty productive zone in combination with extremely fast turn over rates make this unexpected high production per unit area possible. The shortest C turn over time of all samples was 0.3 days.

Phytoplankton net production amounts to a calculated 5 t C per hectare and year.

Derived from primary production data, a theoretical fish production of 100 kg/ha/year can be estimated, which would allow yearly catches of at least 10 to 20 kg per hectare for human consumption without provocing ecological disturbances.

7. Resumo

Quatro investigações limnológicas foram realizadas em épocas diferentes durante os anos 1968 e 1969 na parte inferior do Rio Tapajós.

Os parâmetros físicos e químicos correspondem em geral com resultados anteriores de outros autores. A parte média do rio não mostra uma estratificação do corpo d'água. Em algumas partes do rio ocorrem distintos aumentos de pH, temporariamente causados pela atividade do fitoplancton.

Algumas espécies de Cyanophyceae e Diatomeae formam a maioria do fitoplancton com respeito a quantidade. Chlorophyceae, Desmidiaceae e outros algas são caracterizadas por uma alta diversidade de espécies, mas somente aparecem em densidades baixas ou moderadas. Apesar da baixa concentração encontrada nos nutrientes, a produção do fitoplancton é alta, o que pode ser atribuido às condições excelentes de luz no rio. A produção liquida de 2,4 g $C/m^2/d$ supera muito a taxa de produção dos lagos da várzea, embora as densidades de produção sejam baixas. Uma zona enorme de produtividade em combinação com taxas de "turn over" extremamente rápidas, possibilitam que esta produção inesperada por área seja tão alta. O tempo mais curto do "turn over" do C encontrado em todas amostras foi de 0,3 dias.

A produção liquida de fitoplancton atinge 5 t C calculados por hectare e ano.

Derivado dos dados da produção primária, uma produção téorica de 100 kg/ha/ano de peixe pode ser estimado, o que permitiria no mínimo uma pesca de 10 até 20 kg por hectare para o consumo humano sem provocar distúrbios ecológicos.

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